New Pedetidae (Rodentia: Mammalia) from the Mio-Pliocene of Africa

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New Pedetidae (Rodentia: Mammalia) from the Mio-Pliocene of Africa

Nuevos Pedetidae (Rodentia: Mammalia) del Mio-Plioceno de Africa

M. Pickford[1], P. Mein[2]

ABSTRACT

Pedetidae, or springhares, are represented by a single extant genus (*Pedetes*) and five extinct ones (*Parapedetes, Megapedetes, Propedetes, Rusingapedetes* and *Oldrichpedetes* of which the latter two are new). The fossil record of pedetids tends to be scanty, but remains have been found in Southern Africa, East Africa, the Maghreb, the Arabian Peninsula, Turkey and Greece. Most of the localities have yielded only a few isolated teeth. We here describe some of the abundant fossil material from Namibia and Kenya, which throws a great deal of light onthe family.

Key words: Spring hares, Rodentia, Neogene, Africa, Europe, systematics, biogeography

RESUMEN

Los Pedetidae o liebres saltadoras están representados por un solo género actual (*Pedetes*) y 5 extintos (*Parapedetes*, *Megapedetes*, *Propedetes*, *Rusigapedetes* y *Oldrichpedetes*, estos dos últimos son nuevos). El registro fósil de los pedétidos es escaso, pero restos fósiles han sido encontrados en Sudáfrica, África del Este, Magreb, Península Arábiga, Turquía y Grecia. La mayoría de las localidades sólo han suministrado unos pocos dientes aislados. En el presente trabajo describimos parte del abundante material fósil procedente de Namibia y Kenia, que arroja nueva luz al conocimiento de la familia .

Palabras Clave: Liebres saltadoras, Rodentia, Neógeno, África, Europa, sistematica, biogeografía

Introduction

Springhares or Pedetidae are an African family of superficially kangaroo-like rodents characterised by hystricomorphy (enlarged infraorbital foramen) combined with a sciurognathic mandible, by the bilophodont cheek teeth and the special adaptation for bipedal saltatorial locomotion. They should not be confused with other bilophodont rodents such as *Diatomys* from Thailand, as was already highlighted by Leonard Ginsburg and one of the authors (Mein & Ginsburg, 1997) who erected the family Diatomyidae for it. This paper is dedicated to the memory of Leonard Ginsburg.

There is a single extant genus *Pedetes* represented by two species, *Pedetes capensis* in South Africa, and *Pedetes surdaster* in East Africa (Fig. 1) (the latter is often considered to be a synonym of the former, the position adopted in this paper). Three extinct genera have been described, *Parapedetes* Stromer, 1922, *Megapedetes* MacInnes, 1957, and *Propedetes* Mein & Pickford, 2008. Of these only *Propedetes* is closely related to the extant genus. We here describe two new genera and species of the family.

Parapedetes is known from only one locality, Elisabethfeld, Sperrgebiet, Namibia, an Early Miocene site aged ca 20-21 Ma. Hopwood (1929) recorded its presence at Langental, but the specimen he mentioned is more properly attributed to *Propedetes efeldensis*. *Parapedetes namaquensis* was a small, extremely hypsodont spring hare, and only

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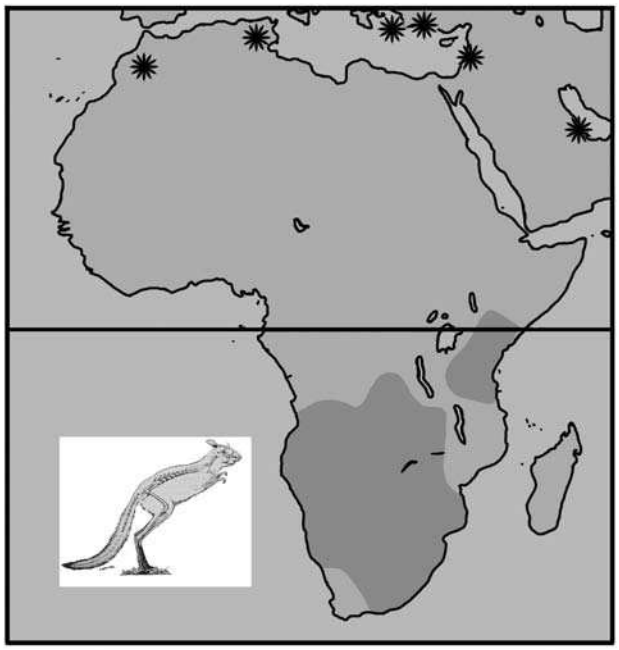

Fig. 1.—Distribution of extant *Pedetes* in South and East Africa (dark grey) and some pedetid fossil localities (black stars) in the Northern Hemisphere (base map from MacDonald, 2001) and reconstitution of *Parapedetes* from Namibia from Stromer (1926).

aged individuals developed roots in the cheek teeth and secreted some cementum. In adults the two lophs are connected longitudinally. There is a mesoflexus in the upper teeth and a hypoflexid in lower cheek teeth. Unworn teeth in the samples collected by the Namibia Palaeontology Expedition reveal that *Parapedetes* exhibit two flexi and two stria of very unequal dimensions, the shallower flexus soon disappearing with even a small degree of wear.

Megapedetes was first described from Songhor, Kenya, an Early Miocene site aged ca 20 Ma. The teeth are not hypsodont but semi-hypsodont. The crown height is roughly equivalent to the length of the tooth. At Arrisdrift, in deposits aged ca 17.5 Ma two species of *Megapedetes* were described by Mein & Senut (2003) *M. gariepensis*, which is relatively common, and *M. pickfordi*, which is rarer. The latter is here attributed to the new genus *Oldrichpedetes*. The cheek teeth of *M. gariepensis* are 10% smaller than those of *M. pentadactylus* (the type species from East Africa) and the molar crowns are slightly more hypsodont, the hypsodonty index H/L (height / length) being 1.3 in lower teeth and 1.5 in upper teeth. In occlusal view the anterior lophid of p/4 is narrower and shows an elongated longitudinal groove on its distal wall. The posterior lophid of m/3 is more transversely developed and among the mandibles collected, one specimen (GSN AD 214'99) exhibits a supernumary tooth (m/4) the first time that such a dental abnormality has been described in Pedetidae.

The genus *Megapedetes* is represented at a number of other localities in East Africa, North Africa, the Arabian Peninsula, Turkey and Greece (Fig. 1). In the last three countries the fossils have been attributed to *Megapedetes aegaeus* (Sen, 1977).

Oldrichpedetes brigitteae nov. gen. nov. sp. from Zebra Hill, Namib-Naukluft Park, Namibia, is the smallest pedetid known. It is represented by an isolated m/1 in which the mesostriid is considerably taller than the hypostriid and the hypsodonty index is 2.4. *Oldrichpedetes pickfordi* from Arrisdrift is known by six teeth. The hypsodonty index is 1.9 and there is a difference in height of the mesostriid and hypostriid of 1.3 mm, making it intermediate between *Megapedetes* and *Propedetes*. The last record of the genus *Oldrichpedetes* is from the Early Pliocene of Tunisia (Batik & Fejfar, 1990).

Rusingapedetes nov. gen. is currently known only from Rusinga Island, Kenya, from deposits aged about 17.8 Ma. Previously, isolated teeth of this genus were attributed to a small, un-named species of *Megapedetes* (Lavocat, 1973) but now that a complete skull is known it is clear that it represents an undescribed genus of pedetid.

In the aeolianites of Rooilepel and related sites in the Sperrgebiet, Namibia, there are abundant teeth, jaws and damaged skulls, and occasional articulated skeletons, attributed to the genus *Propedetes*, first described from Elisabethfeld (Mein & Pickford, 2008). The post-cranial bones indicate that it was well adapted to saltatorial locomotion. The type species, *Propedetes efeldensis*, is about the same size as *Parapedetes namaquensis*, and is equally hypsodont. Cementum may appear at the base of the mesostria in senile individuals, when short roots are developed. The mesostria(id) is considerably taller than the hypostria(id). In *Parapedetes*, the opposite is the case, the hypostria(id) being considerably taller than the mesostria(id). In *Megapedetes* and *Oldrichpedetes*, the mesostria(id) and hypostria(id) are about the same height as each other.

In *Propedetes* the lower p/4 is less hypsodont than the molars and its morphology is different. In contrast to *Parapedetes*, and similar to *Pedetes*, some of the teeth of *Propedetes* are strongly curved, especially the P4/ which is concave anteriorly, and

Table 1.—**List of fossil pedetid localities (with latitude and longitude according to Google Earth) and taxa arranged by country. Where necessary the species names have been updated from the original names mentioned in the literature. Several new species of *Propedetes* occur in Namibia, and will be described in a forthcoming paper**

SOUTHERN AFRICA

South Africa

Florisbad (28°52'25"S: 25°36'12.9"E) *Pedetes hagenstadti* (Dreyer & Lyle, 1931).
Kramleeg (30°17'05.8"S: 17°17'24.0"E) *Pedetes* cf *capensis* (this paper)
Sterkfontein (26°0'56.5"S: 27°44'4.7"E) *Pedetes* sp. (this paper).
Swartkrans (26°01'02"S: 27°43'24.7"E) *Pedetes* cf *capensis* (Brain, 1993).
Taung (Equus Cave) (27°37'09"S: 24°38'59"E) *Pedetes gracilis* (Broom, 1930, 1934, 1939; McKee, 1994).

Namibia

Arrisdrift (28°28'32.8"S: 16°42'23.2"E) *Megapedetes gariepensis*, *Oldrichpedetes pickfordi* (Mein & Senut, 2003).
Awasib (25°18'19"S: 15°38'57"E) *Pedetes* cf *gracilis* (this paper).
Berg Aukas (19°30'57.5"S: 18°15'10.5"E) *Propedetes laetoliensis*, *Pedetes* cf *capensis* (this paper)
Bushman Hill (west of) (25°08'00.4"S: 15°44'28.9"E) *Pedetes gracilis* (this paper).
Daberas Dune near inselberg (28°08'35"S: 16°39'40"E) *Pedetes gracilis* (this paper).
Ekuma (18°37'06.9"S: 16°00'59.1"E) *Propedetes laetoliensis* (Pickford *et al*., 2009).
Elisabethfeld (26°58'52.5"S: 15°15'57.1"E) *Parapedetes namaquensis* (Stromer, 1922, 1926) *Propedetes efeldensis* (Mein & Pickford, 2008).
GP Pan North (28°29'47.3"S: 16°32'14.7"E) *Propedetes* cf *laetoliensis* (this paper).
Harasib (19°34'02"E: 17°48'19.3"E) *Propedetes* sp. nov. (Mein *et al*., 2000).
Karingarab (28°12'15"S: 16°21'30"E) *Propedetes laetoliensis* (this paper).
Langental (27°24'27.9"S: 15° 24'27.9"E) *Propedetes efeldensis* (Hopwood, 1929; Mein & Pickford, 2008).
Rooilepel (28°17'56.4"S: 16°35'01"E) *Propedetes efeldensis*, *Propedetes* sp. nov., *Propedetes laetoliensis* (Corbett, 1989; this paper).
Tree Pan (25°54'40.6"S: 15°56'09.9"E) *Pedetes* cf *gracilis* (this paper).
Tsauchab (24°30'14.4"S: 15°43'01.4"E) *Pedetes laetoliensis*, *Pedetes* cf *capensis* (this paper).
Zebra Hill (23°37'40.2"S: 15°38'42.7"E) *Oldrichpedetes brigitteae* gen. et sp. nov. (this paper).

Botswana

Koanaka N (20°08'38.3'S: 21°12'33.9"E) *Pedetes capensis* (this paper).
Koanaka W (20°09'31.5"S: 21°11'40.1"E) *Pedetes capensis* (this paper).

Zimbabwe

Bulawayo (20°10'10.5"S: 28°40'58.8"E) *Pedetes capensis* (Zeally, 1916).

EASTERN AFRICA

Kenya

Chamtwara (0°07'35.8"S: 35°15'58.8"E) *Megapedetes pentadactylus* (Pickford, 1986).
Fort Ternan (0°13'10.6"S: 35°20'22.7"E) *Megapedetes* cf *pentadactylus* (Denys & Jaeger, 1992).
Gamble's Cave (0°39'S: 36°13'E) *Pedetes* sp. (Hopwood, 1931).
Isinya (1°41'01.4"S: 26°51'10.2"E) *Pedetes capensis* (Brugal & Denys, 1989).
Kipsaraman (0°44'57.7"N: 35°49'28.0"E) *Megapedetes aegaeus* (Winkler, 1992, 2002).
Kalodirr (3°19'01.8"N: 35°44'51"E) ?*Megapedetes aegaeus* (Winkler, 1992).
Kirimun (0°43'58.8"N: 36°53'32"E) *Megapedetes aegaeus* (Ishida & Ishida, 1982).
Lainyamok (1°48'05.8"S: 36°12'31.9"E) *Pedetes* sp. (Potts & Deino, 1995).
Legetet (0°08'40.2"S: 35°15'24.5"E) *Megapedetes pentadactylus* (Pickford, 1986).
Lukeino (0°45'12.7"N: 35°52'29.9"E) OCO Bar 602'02, lower incisor, *Propedetes* sp. (Mein & Pickford, 2006).
Maboko (0°09'40.1"S: 34°36'26.7"E) *Megapedetes gariepensis* (Winkler, 1992).
Magare Beach (0°20'56.4"S: 34°16'26.1"E) *Megapedetes* (Pickford, 1986).
Meswa Bridge (0°08'09.3"S: 35°12'18.6"E) *Oldrichpedetes praecursor* (Winkler, 1992).
Mfwangano (Makira, Walangani and Hiwegi Formations) (0°27'37.3"S: 34°03'40.1"E) *Megapedetes pentadactylus* (Pickford, 1986).
Ombo (0°04'04.8"S: 34°33'50.7"E) *Megapedetes* small sp. (Pickford, 1986).
Rusinga (Wayondo and Hiwegi Formations) (0°24'27.7"S: 34°12'39.5"E) *Megapedetes pentadactylus*, *Rusingapedetes tsujikawai* gen. et sp. nov., (Lavocat, 1973; MacInnes, 1957; Pickford, 1986; this paper).
Songhor (0°02'06.5"S: 35°12'34.6"E) *Megapedetes pentadactylus* (Lavocat, 1973; MacInnes,1957; Pickford, 1986).

Uganda

Moroto II (2°40'22.1"N: 34°42'54.6"E) *Megapedetes gariepensis* (Mein & Pickford, 2006).
Napak I (2°06'02.4"N: 34°11'27.1"E) *Megapedetes pentadactylus* (Lavocat, 1973; MacInnes, 1962).
Napak IV (2°07'03.6"N: 34°11'17"E) *Megapedetes pentadactylus* (MacInnes, 1962).
Napak V (2°06'43.7"N: 34°11'15.6"E) *Megapedetes pentadactylus* (MacInnes, 1962).
Bukwa (1°17'06.3"N: 34°47'04.98"E) *Megapedetes pentadactylus* (Walker, 1969).

Tanzania

Eyasi (3°32'31.6"S: 35°14'32.7"E) *Pedetes capensis* (Dietrich, 1939).
Laetoli (3°13'10"S: 35°10'17"E) *Propedetes laetoliensis* (Davies, 1987; Dietrich, 1942), *Pedetes* cf *surdaster* (Davies, 1987).
Olduvai (2°56'58.9"S: 35°14'32.7"E) *Pedetes* sp.
Peninj (2°19'14.1"S: 35°53"5.4"E) *Pedetes* sp.

Table 1 *(continued).*—**List of fossil pedetid localities (with latitude and longitude according to Google Earth) and taxa arranged by country. Where necessary the species names have been updated from the original names mentioned in the literature. Several new species of *Propedetes* occur in Namibia, and will be described in a forthcoming paper**

NORTHERN AFRICA AND ARABIA

Morocco
Beni Mellal (32°18'47.3"N: 6°21'25"E) MN 6, *Megapedetes aegaeus* (Lavocat, 1961).

Tunisia
Ech Chouachi (35°33'45"N: 9°32'21.7"E) MN 14, *Oldrichpedetes fejfari* gen. et sp. nov. (Batik & Fejfar, 1990).

United Arab Emirates
As Sarrar (26°59'10.5"N: 48°23'58.2"E) MN 5, *Megapedetes gariepensis*, *Megapedetes aegaeus* (Thomas *et al*., 1982).

Israel
Rotem (30°48'44"N: 34°50'43"E) *Megapedetes* sp., (Tchernov *et al*., 1987; Wood & Goldsmith, 1998).

EUROPE

Turkey
Bayraktepe (37°01'28"N: 36°46'01"E) MN 7/8, *Megapedetes aegaeus* (Sen, 1977).

Greece
Chios (38°18'35.3"N: 26°08'43.7"E) MN 5, ?*Megapedetes pentadactylus* (Tobien, 1968; Sen,1977).

the m/3 which is concave buccally and posteriorly. In this genus the determination of isolated teeth follows the same rules as for *Megapedetes*.

Broken teeth from Rooilepel show a strange undulation at the base of the flexus creating a central isthmus (Fig. 4). It is not possible to observe this structure in complete teeth. This formation is present in all the broken teeth examined, but unfortunately we have not been able to see it in other species.

Abundant specimens of *Propedetes* have been found associated with struthious eggshells which permit them to be correlated to the biochronological time scale, from which their ages can be estimated (paper in preparation). The main horizons are the *Tsondabornis minor* level (21-18 Ma) from which *Parapedetes namaquensis*, *Propedetes efeldensis* and *Megapedetes gariepensis* are known, the *Diamantornis corbetti* levels (base of the Middle Miocene, ca 16 Ma), the *Diamantornis wardi* levels (top of the Middle Miocene, ca 12-10 Ma) and the *Diamantornis laini* levels (Late Miocene, ca 8-6 Ma) which have yielded more evolved, more hypsodont species of *Propedetes*. Throughout this period hypsodonty increased, culminating in *Propedetes laetoliensis*, which, in addition to its type locality in Tanzania has been collected in Namibia at Berg Aukas, Karingarab, GP Pan North, Rooilepel, Tsauchab and Ekuma (Etosha).

Pedetes laetoliensis (Davies, 1987) was defined on the basis of fossils from the Middle Pliocene of Laetoli, Tanzania. It is here transferred to the genus *Propedetes* because of the morphology of the p/4 and the presence in the species of rooted cheek teeth – in *Pedetes* the cheek teeth are arhizic. *Propedetes laetoliensis* is larger than earlier species of *Propedetes* from the *Diamantornis laini* levels, and cementum is abundant in the mesostria(id) and reaches the occlusal surface.

Pedetes is characterised by rootless cheek teeth and a molariform p/4. The hypsodonty of the P4/ increased rapidly with the passage of geological time. In the extant form this tooth is inclined along the premaxillary bone. In *Pedetes gracilis* from Taung, South Africa (Middle Pliocene), the P4/ was less curved and more upright. In Namibia the same extinct species has been collected at Bushman Hill, Daberas Dune (near the inselberg) and Tree Pan. Fossils of the extant species, *Pedetes capensis* have been found in Namibia at Tsauchab and at other sites in South Africa and Botswana (Table 1).

In *Pedetes* the existence of a second flexus in the cheek teeth was demonstrated by Wood (1962, 1965) but for an inexplicable reason, lateral views of young *Pedetes* teeth have never been illustrated. The mesostria (and striids) are so tall that they encompass the entire height of the tooth and cementum occurs in the resulting canal, even in juvenile individuals.

Nomenclature of the teeth of Pedetidae

The cheek teeth of pedetids are comprised of two lophs (lophids) separated by a median transverse valley (Fig. 2, 3, 4). On the buccal and lingual surfaces the valley is expressed as notches or deep

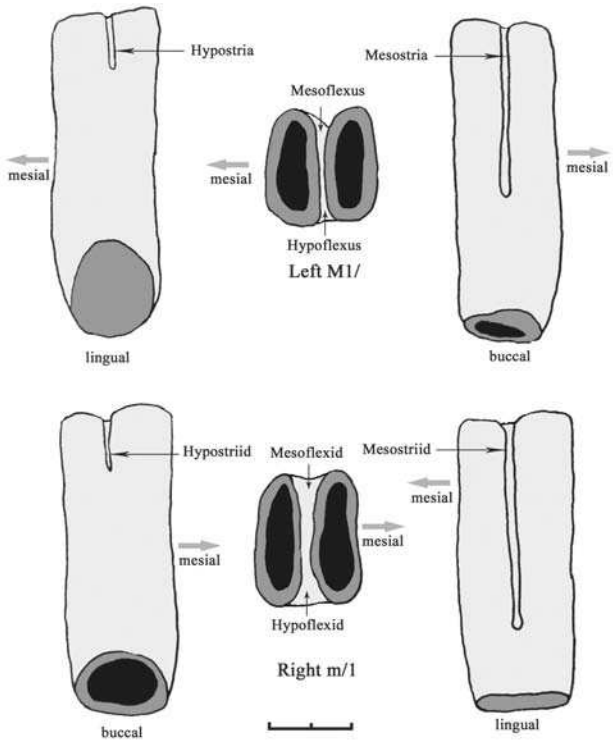

Fig. 2.—Nomenclature of pedetid cheek teeth employed in this contribution.

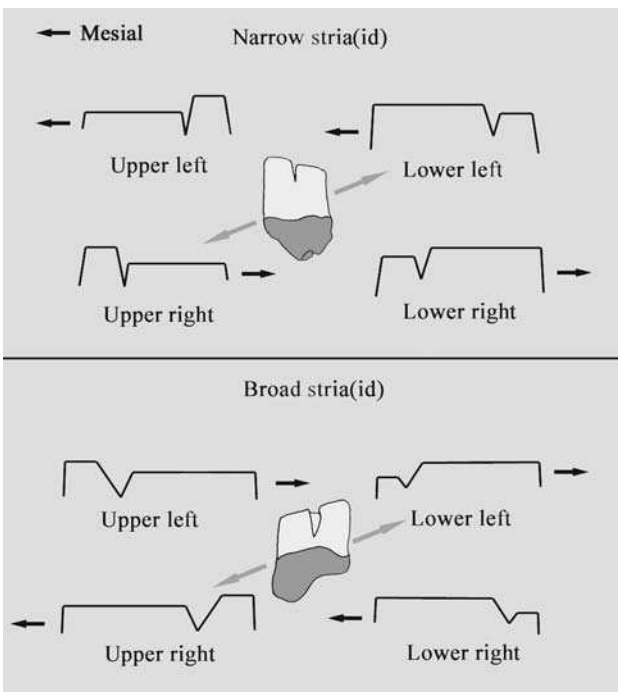

Fig. 3.—Orientation of pedetid cheek teeth and determination of meristic position.

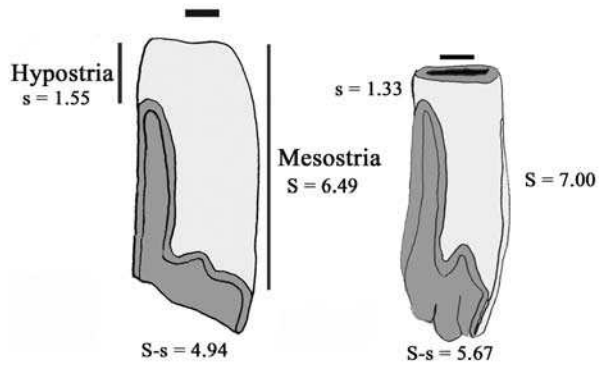

Fig. 4.—GSN RL 31'96l (left) internal view of the anterior loph of a left P4/ of *Propedetes* from the *Diamantornis wardi* levels at Rooilepel, Namibia (S-s = 4.94) which split down the middle, showing the different heights of the stria, and also the presence of an isthmus in the middle of the mesoflexus, and GSN RL 31'96m (right) internal view of posterior loph of a more hypsodont right M2/ (S-s = 5.67) of *Propedetes laetoliensis* with a taller isthmus (scale bars – 1 mm).

grooves, which, following the nomenclature of Stirton (1935) are called the hypostria(striid) and mesostria(striid). The hypostria(striid) (s) is always narrower than the mesostria(striid) (S). The first loph(id) is always more developed mesio-distally than the second loph(id) on the hypostria(striid) side. The determination of isolated teeth of *Propedetes* is thus done as follows (Fig. 2, 3, 4):

With the stria(id) oriented vertically and the occlusal surface upwards

1. the anterior loph (id) is longer than the distal one (black arrows in figure 3).

2. upper cheek teeth have a higher distal loph than the mesial one; lower cheek teeth have a lower distal lophid than the mesial one.

Because of the simple bilophodont structure of the cheek teeth it is not easy to determine the meristic position of isolated specimens. In occlusal view the two lophs are more convergent on one side which results in a narrower flexus (hypoflexus) (s) which is lingual in upper teeth and buccal in lower teeth (hypoflexid). On the other side of the crown, the flexus (mesoflexus) is antero-posteriorly longer (S).

In summary, the discrimination of pedetid teeth is based, first and foremost, on the different heights of the mesostria(id) and hypostria(id) in the intermediate molars (M1/ and M2/, m/1 and m/2), secondly, on the maximum ratio of height over length (H/L) which represents the hypsodonty, and thirdly, on the crown area (length x breadth), and in *Propedetes* on the measure S-s.

Fig. 5.—Distribution of fossil Pedetidae.

Abbreviations

AD - Arrisdrift, Bar – Baringo, Kenya, bld – distal bucco-lingual breadth, blm – mesial bucco-lingual breadth, GSN - Geological Survey of Namibia, H – height, H/L – ratio height to length, KNM - Kenya National Museum, L – length, MDL – mesio-distal length, ME - Meswa Bridge, MN – Mammal Neogene (mammal zones of Europe), OCO – Orrorin Community Organisation, Kenya, RU – Rusinga, RL – Rooilepel, S – tall stria(id), s – short stria(id), S-s – difference in height between the tall and short stria(ids), ZH - Zebra Hill.

The meristic position of teeth is abbreviated by the use of capital and lower case letters for upper and lower teeth respectively and by the position of the forward slash - / - relative to the number. Above the slash the number denotes an upper tooth (e.g. P4/, M2/) whereas below the slash it denotes a lower tooth (e.g. p/4, m/3).

Previous literature

Pedetid fossils have been reported on many occasions, yet a complete listing of the available samples has not previously been compiled. The following table and figures (Table 1, Fig. 5, 6) provide a list of localities and taxa gleaned from the literature as well as of undescribed material collected by the authors. Some of the fossils mentioned in the literature could not be studied, either due to the fact that the material has been lost since being published, or because its current whereabouts are unknown.

Systematic descriptions

Order Rodentia Bowdich, 1821
Family Pedetidae Gray, 1825
Subfamily Pedetinae Gray, 1825

Genus *Rusingapedetes* nov.

Type species: *Rusingapedetes tsujikawai* nov.

Diagnosis: Small pedetid with brachyodont cheek teeth, from ventral to dorsal the anterior margin of orbit slopes strongly mesially.

Derivatio nominis: The genus name refers to the type locality, Rusinga, Kenya.

Species *Rusingapedetes tsujikawai* nov.

Holotype: KNM RU 14355, skull with deeply worn cheek dentition (Fig. 7, 8, 10).

Paratypes: KNM RU 2347, left p/4, KNM RU 2348, left m/1; KNM RU 2349, lower molar (Lavocat, 1973, pp. 197-198, pl. 28, fig. 10) (Fig. 9).

Type locality: R1, Rusinga Island, Kenya.

Age: Early Miocene, ca 17.8 Ma.

Diagnosis: Small size, strongly brachyodont cheek teeth, M3/ not reduced.

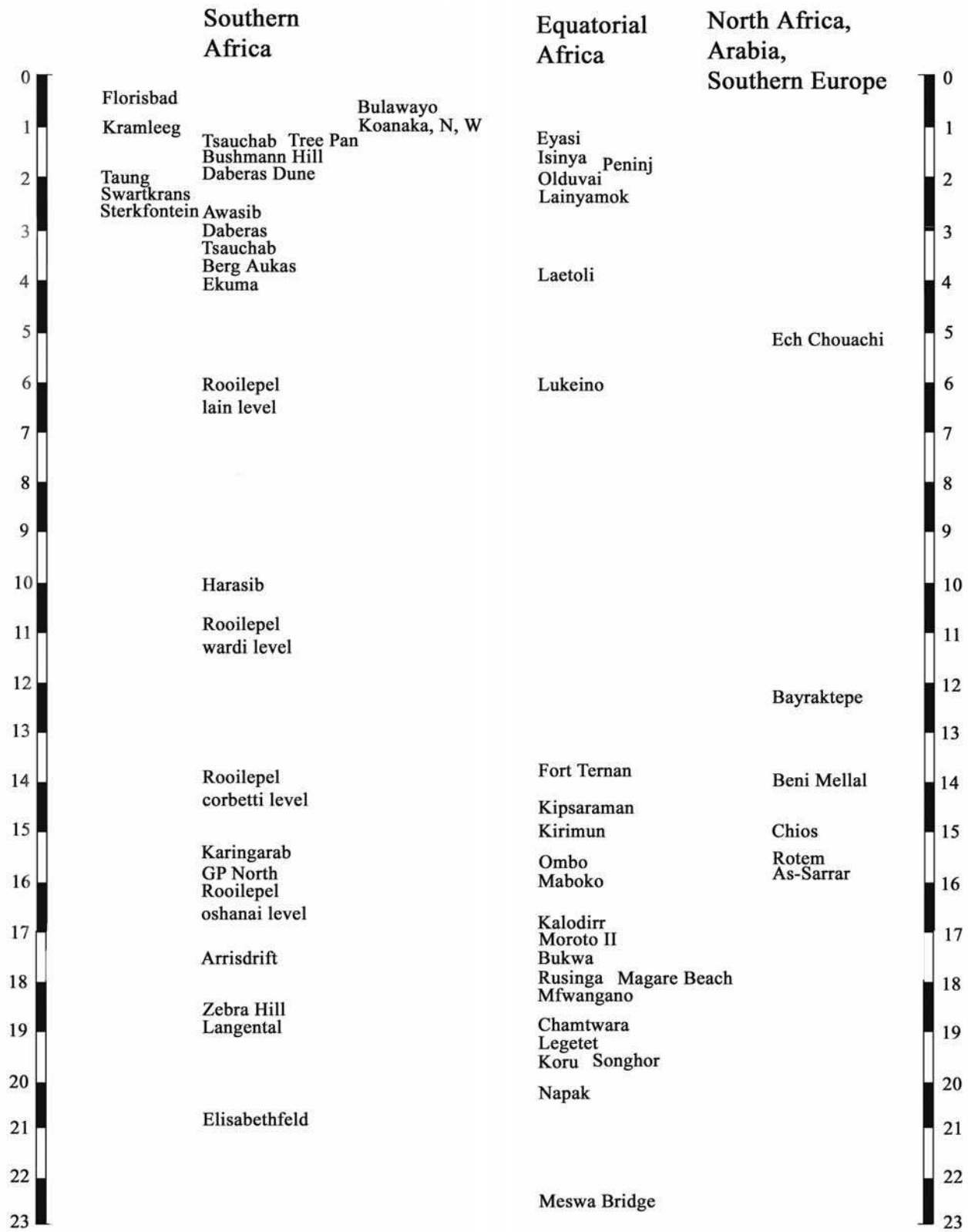

Fig. 6.—Stratigraphic position and approximate ages of fossil Pedetidae localities.

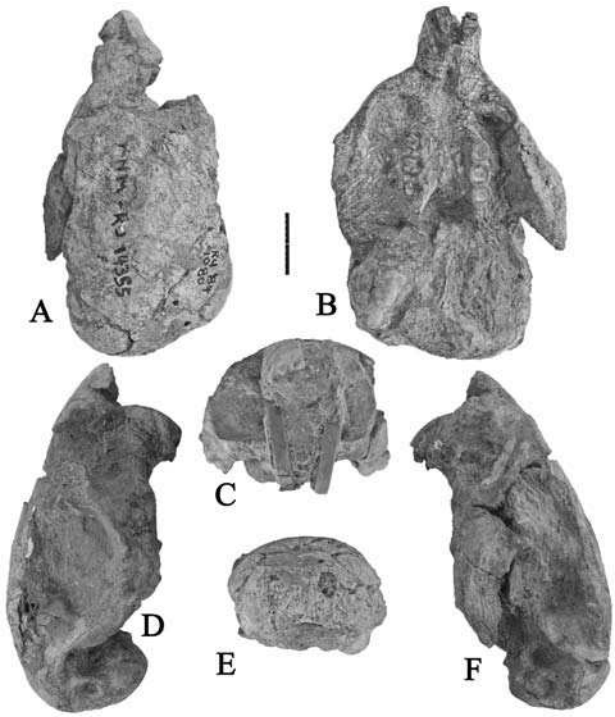

Fig. 7.—Holotype skull of *Rusingapedetes tsujikawai* nov. gen. nov. sp. KNM RU 14355, A) dorsal, B) palatal, C) anterior, D) right lateral, E) posterior and F) left lateral views (scale 10 mm).

Derivatio nominis: The species name is in honour of Dr Hiroshi Tsujikawa who kindly provided information valuable for this study.

Description: The holotype skull of *Rusingapedetes tsujikawai* represents a senile individual with heavily worn cheek teeth (Fig. 7, 8, 10). The skull has been slightly distorted by post-mortem processes, it is ca 5 cm long, and ca 3.5 cm at its broadest measured across the zygomatic arches. The cheek tooth row is 10.6 mm long and consists of only three teeth on each side, which we interpret to be the M1/ to M3/, although the anterior tooth is less worn than the two teeth behind it suggesting that the teeth may instead be the P4/ to M2/. There is no sign of alveoli behind the distal teeth but there may be a resorbed alveolus in front of the anterior one on the left side. Further preparation or scanning is required to resolve the uncertainty.

The skull possesses many characteristics of pedetids (skulls are known for *Pedetes capensis*, *Parapedetes namaquensis*, *Megapedetes pentadactylus* and *Propedetes laetoliensis*) (Fig. 10). The rounded extensions of the supra-tympanic part of the auditory bullae are vast, and encroach onto the dorso-lateral aspect of the skull at the rear, where they are separated from each other by the inter-parietal and supra-occipital (Fig. 7). The incisors are opisthodont and rectangular in section, the skull is hystricomorph, the dorsal surface of the brain case is broad with no sign of a sagittal crest, the nasals are large and overhang the upper incisors, and the external auditory meatus is roughly at mid-height of the rear of the skull.

The specimen differs from the skull of *Pedetes* and *Propedetes* by its smaller dimensions, by the forwardly sloping margin of the infraorbital margin (upright in *Pedetes, Megapedetes, Parapedetes* and *Propedetes*) and the upper incisors diverge more rapidly as they curve upwards and backwards into the premaxilla. The posterior choanae in the fossil extend anteriorly between the M2/s as in *Pedetes*; in *Propedetes* they reach even further forwards to the M1/s (Davies, 1987, fig. 6-28).

Rusingapedetes differs from *Megapedetes* by its much smaller dimensions, the anteriorly sloping anterior and mesio-distally broader orbital margin. *Rusingapedetes* differs from *Parapedetes* by its greater dimensions, by its forwardly sloping infraorbital margin, and by its brachyodont cheek teeth endowed with roots, and by the loss of P4/ in aged individuals.

The orbit in *Rusingapedetes* seems to be small relative to the dimensions of the skull compared to those of *Pedetes*, *Megapedetes*, *Parapedetes* and *Propedetes*. This suggests that it may

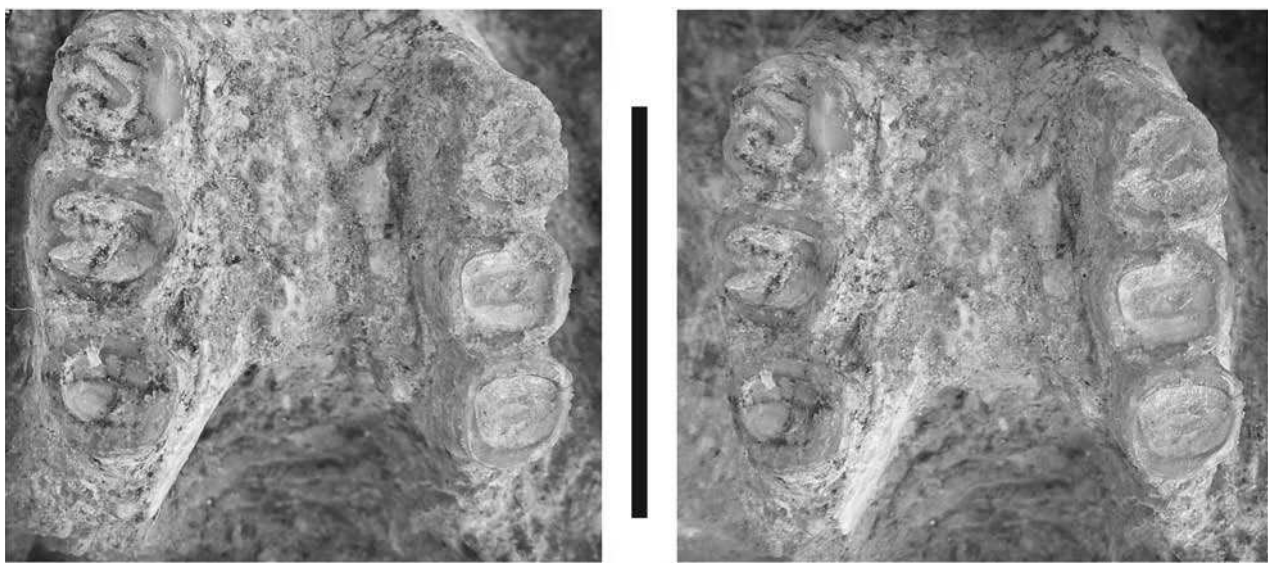

Fig. 8.—Stereo occlusal image of the palate of KNM RU 14355, holotype of *Rusingapedetes tsujikawai* nov. gen. nov. sp. (scale 10 mm).

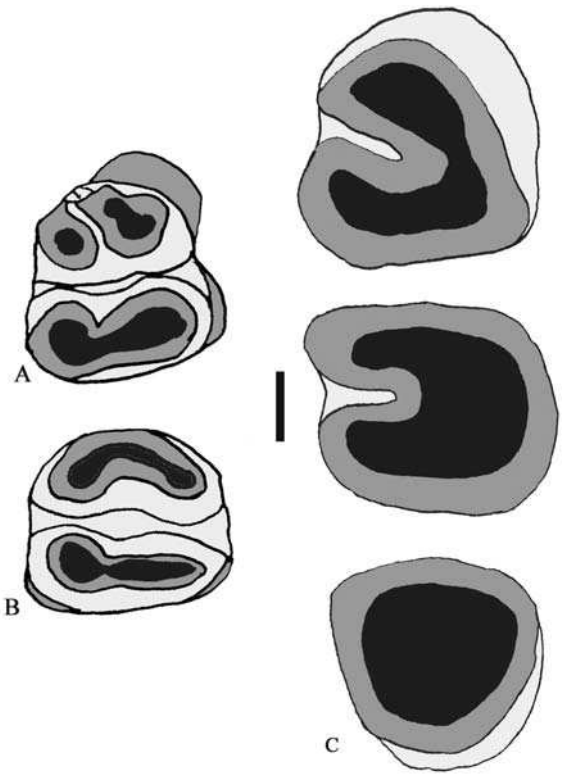

Fig. 9.—Teeth of *Rusingapedetes tsujikawai*, nov. gen. nov. sp. The specimens on the left, A) KNM RU 2348, left m/1, occlusal view, and B) KNM RU 2347, left p/4, occlusal view, were described by Lavocat (1973) but their current whereabouts are unknown. The teeth to the right, C) are of the holotype, KNM RU 14355.

Table 2.—**Measurements (in mm) of the teeth of *Rusingapedetes tsujikawai* nov. gen. nov. sp.**

Specimen	Tooth	MDL	blm	Bld
KNM RU 2348	m/1 left	2.70	3.50	-
KNM RU 2347	p/4 left	2.83	2.63	-
KNM RU 14355	M1/ right	3.40	3.40	-
KNM RU 14355	M2/ right	2.85	3.60	-
KNM RU 14355	M3/ left	2.80	3.20	2.20
KNM RU 14355	M3/ right	3.00	2.90	-

have been more diurnal than the other taxa. The first is an obligate nocturnal animal and the others may have been the same.

There are only three cheek teeth preserved in each maxilla in the skull, which we interpret to be the three molars (Table 2). There is a hint of the presence of a resorbed alveolus in front of M1/ which needs to be verified by further preparation of the specimen. The teeth in the holotype skull are deeply worn. There is a prominent mesoflexus on the buccal side of the M1/ and M2/, but M3/ is worn so deeply that no sign of the mesoflexus is left. If there were a hypoflexus, then it has been worn away in all the teeth. A superficial glance at the teeth gives the false impression that they are somewhat like those of bathyergids.

Genus *Oldrichpedetes* nov.

Type species: *Megapedetes pickfordi* Mein & Senut, 2003

Diagnosis: Pedetidae of medium size, cheek teeth with straight columnar crowns, stria and striids oriented as in *Mega-*

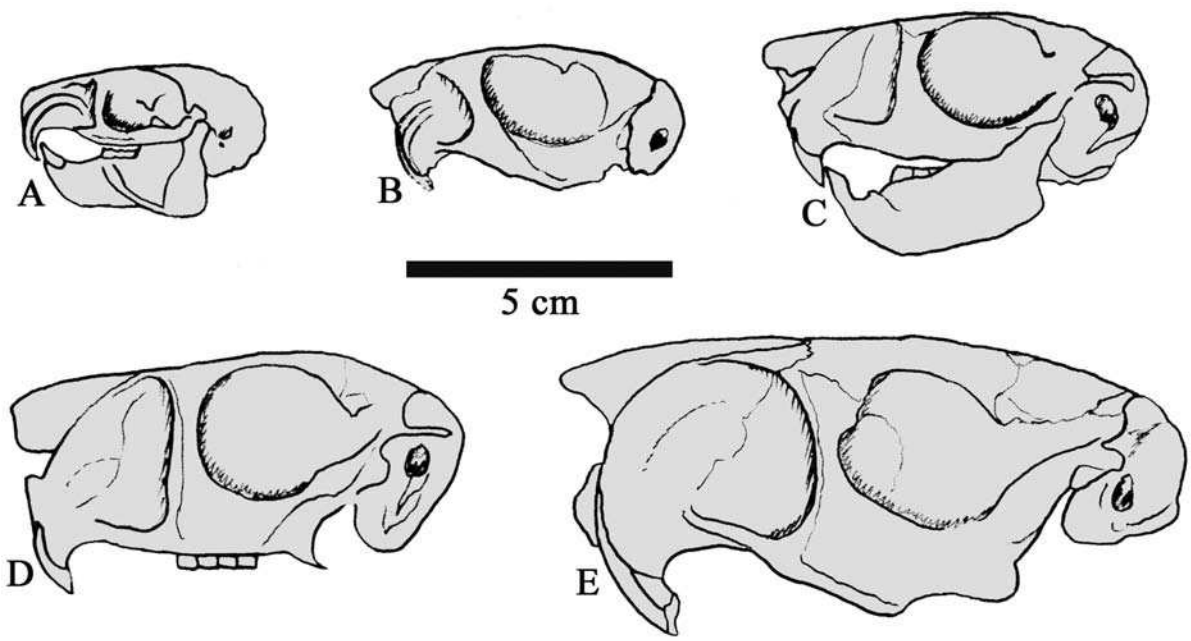

Fig. 10.—Comparison of lateral views of the skulls of fossil and extant pedetids. A – *Parapedetes namaquensis*, B – *Rusingapedetes tsujikawai* nov. gen. nov. sp., C – *Propedetes laetoliensis*, D – *Pedetes capensis*, E – *Megapedetes pentadactylus*. Note the orientation of the anterior margin of the orbit (scale – 5 cm).

Table 3.—**Measurements (in mm) of the teeth of *Oldrichpedetes pickfordi* (Mein & Senut, 2003).**

Specimen	Tooth	MDL	Blm	bld	H	S	S	H-s/L	H-S/L	S-s	H/L
GSN AD 583b'94	m/1 right	2.73	3.13	3.05	3.85	1.53	0.66	1.20	0.80	0.87	1.40
GSN AD 273b'96	m/2 left	2.65	3.00	2.65	3.78	1.53	1.10	1.00	0.80	0.43	1.40
GSN AD 583a'94	m/2 left	2.55	2.80	2.80	4.88	3.25	1.98	1.10	0.60	1.27	1.90
GSN AD 536'95	m/2 right	2.80	3.00	2.80	3.70	1.34	0.35	1.20	0.80	0.99	1.30
GSN AD 405'99	M1/ right	2.90	2.72	2.95	4.00	1.34	0.60	1.20	0.90	0.74	1.40
GSN AD 715'99	P4/ right	2.84	2.60	2.73	3.80	1.16	0.14	1.30	0.90	1.02	1.30

pedetes and *Propedetes*, short stria(id) lingual in upper teeth, buccal on lower teeth, roots coalescent and can be long in senile teeth. Crown height increased with the passage of geological time but the difference in length of the striids and stria remained weak.

Oldrichpedetes differs from the much larger *Megapedetes* by its greater hypsodonty, the ratio H/L being greater than 1 (in non-senile teeth). *Oldrichpedetes* differs from *Parapedetes* by its greater dimensions and by the inverted heights of the striids. *Oldrichpedetes* differs from *Propedetes* by its straight columnar crowns, not only in buccal and lingual views, but also in mesial and distal views. In *Propedetes* the molars are laterally curved.

Derivatio nominis: The genus name honours Oldrich Fejfar and acknowledges his contribution to the understanding of European and African fossil micromammals.

Included species:

Oldrichpedetes pickfordi (Mein & Senut, 2003), MN 5, ca 17.5 Ma, Arrisdrift, Namibia.

Oldrichpedetes fejfari sp. nov. MN 14, Ech Chouachi, Tunisia. *Oldrichpedetes brigitteae*, sp. nov. ca 18-19 Ma, Zebra Hill, Namibia. *Oldrichpedetes praecursor*, sp. nov. ca 22.5 Ma, Meswa Bridge, Kenya.

Species *Oldrichpedetes pickfordi* (Mein & Senut, 2003)

Holotype: GSN AD 715'99, right P4/ (Mein & Senut, 2003, pl. 2, fig. A)

Paratypes: GSN AD 583a'94, left m/2 (Mein & Senut, 2003, pl.1 fig. 6); GSN AD 273b'96, left m/2 (Mein & Senut, 2003, pl. 1, fig. 5).

Referred material: GSN AD 140'99, left M3/; GSN AD 583b'94, right m/1; GSN AD 536'95, right m/2.

Type locality: Arrisdrift, Namibia, basal Middle Miocene (MN 4) ca 17-17.5 Ma. Original diagnosis. See Mein & Senut, 2003, p. 166.

Emended diagnosis: m/3 with reduced posterior loph.

Complement to original description: Among the various species of *Oldrichpedetes*, *O. pickfordi* is the best represented with 6 teeth. AD 414'00 is here interpreted to be a left m/1 of *Megapedetes gariepensis* because its dimensions are greater than those of other specimens of *O. pickfordi*, and the root is recurved towards the front.

The upper dentition is represented by two teeth (Table 3). The P4/, GSN AD 715'99 (the holotype) has weak basal elongation and the occlusal surface of the crown is very oblique with respect to the column of the tooth. In 2003 the left M3/ was originally attributed to *Megapedetes gariepensis*, but its dimensions are too small for it to belong to this taxon. In Pedetidae, the M3/ and m/3 usually have similar lengths. The description of the specimen remains valid. The tooth is deeply worn, the hypoflexus has disappeared, and the mesoflexus has been transformed into a fossette. Nevertheless the apparent hypsodonty is strong (H/L is ca 1.5) and the single root is curved towards the rear.

The lower dentition is known by three m/1-m/2s and an m/3. The distinction between m/1 and m/2 is based on the fact that m/2 is shorter than m/1. The maximal breadth is at the rear in m/1 and in the front in the m/2. This is why GSN AD 273b'96 is a left m/1, and GSN AD 583b'94 is a right m/1, whereas GSN AD 583a'94 and GSN AD 273b'96 are left m/2s.

In the 2003 publication, no m/3 was identified. It appears that GSN AD 405'99, initially thought to be a right M1/ is in reality a left m/3, because the posterior loph is lower and shorter than the anterior one.

Species *Oldrichpedetes fejfari* nov.

Holotype: Left m/1, Charles University, Prague.

Type locality: Black lacustrine clay with ferruginous nodules south of Ech Chouachi, Central Tunisia (Batik & Fejfar, 1990).

Age: Early Pliocene age (MN 14) based on the associated murids (*Saidomys*, *Tectonomys*, ?*Hansdebruijnia* – reidentified from Batik & Fejfar, 1990).

Diagnosis: Largest and most hypsodont species of *Oldrichpedetes*, in which the buccal and lingual stria/striids are equally tall.

Derivatio nominis: The species name is in honour of Oldrich Fejfar and his extensive studies of Old World micromammals.

Description: The holotype is the only known specimen (Fig. 11, Table 4). The identification of the tooth as a lower molar is based on the observation that the larger of the two lophs slopes anteriorly and at the same time is the taller of the two.

It is a left m/1 or m/2 because of the breadth of the posterior loph relative to the anterior one. The presence of mesial and distal contact facets of similar development pleads in favour of its identification as an m/1, because if it were an m/2 the retarded eruption of the m/3 would result is a smaller distal contact facet. Furthermore, in all pedetids the distal breadth of m/2 is less than its proximal breadth. In this specimen the occlusal breadths are

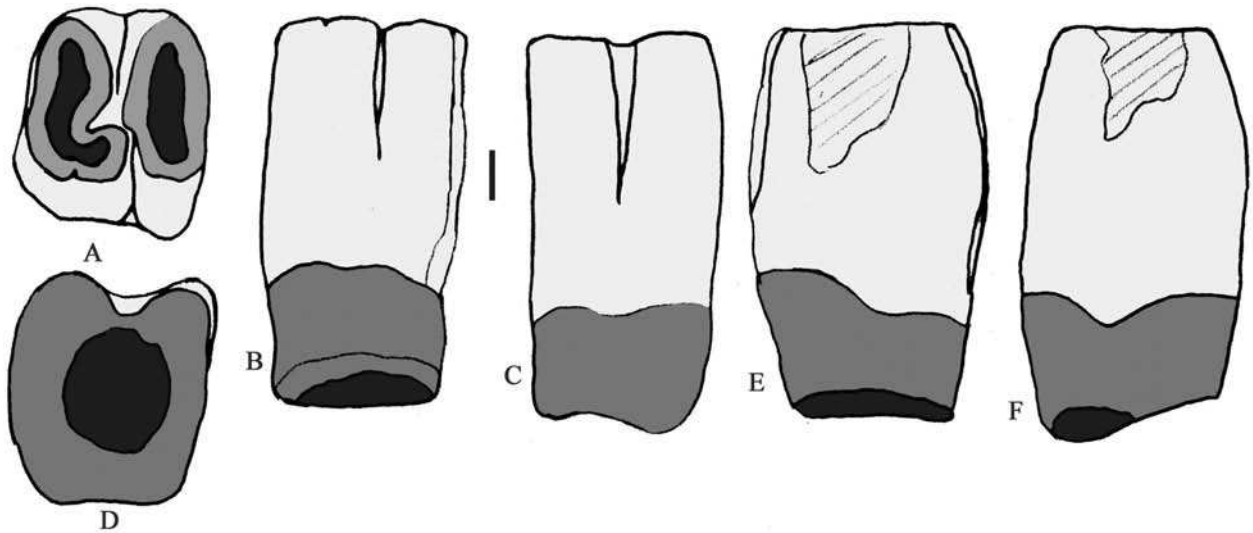

Fig. 11.—Holotype specimen of *Oldrichpedetes fejfari*, nov. gen. nov. sp. from Ech Chouachi, Tunisia, A) occlusal, B) buccal, C) lingual, D) radicular, E) distal, F) mesial views (scale - 1 mm).

Table 4.—**Measurements (in mm) of the tooth of *Oldrichpedetes fejfari* nov. gen. nov. sp. From Ech Chouachi, Tunisia**

Specimen	Tooth	MDL	blm	bld	H	S	s	H-s/L	H-S/L	S-s	H/L
Ech Chouachi	m/1 left	3.82	3.55	3.52	8.40	3.40	2.90	4.60	0.40	0.50	1.30

Measurement/ Position	Mesio-distal length	Bucco-lingual breadth anterior	Bucco-lingual breath posterior
Apex	3.82	3.55	3.57
Base	3.89	4.51	4.57

3.55 and 3.57 and the basal breadths 4.51 and 4.57, which are close, indicating that the tooth is most likely an m/1.

The tooth is juvenile because it had not completed growing, the occlusal dimensions being considerably less than the basal ones.

It is noted that with growth the breadth increases faster than the length. In the original description of the specimen (Batik & Fejfar, 1990) the authors inverted the front and back in the occlusal view. Recall that in all pedetids, when the stria(id) is oriented vertically, the occlusal surface of the upper cheek teeth rises towards the rear, whereas in lower teeth it descends to the rear. The stria and striids subdivide the crown into two lophs, of which the anterior one is longer than the posterior one (both upper and lower molars). Despite its marked hypsodonty, the crown of the Ech Chouachi pedetid molar is columnar and straight.

Species *Oldrichpedetes brigitteae* nov.

Holotype: GSN ZH 1'95, left m/1 or m/2.

Type locality: Zebra Hill, Namib-Naukluft Park, Namib Desert, Namibia.

Age: ca 18-19 Ma, cf Pickford & Senut, 1999, p. xix. Associated with eggshells of *Tsondabornis psammoides* in the Tsondab Sandstone Formation (Pickford, 2009).

Diagnosis: Smallest known species of Pedetidae, buccal striid relatively tall, lingual striid recurved distally towards its base. The specimen has a single root.

Derivatio nominis: The species name is in honour of Brigitte Senut, co-leader of the Namibia Palaeontology Expedition.

Description: The presence of anterior and posterior contact facets indicates that the tooth is an m/1 or an m/2 (Fig. 12, Table 5). The largest loph is also the tallest (even though the difference in height is not very great) which indicates that it is a right tooth. The presence of a single root apically suggests coalescence of the root or taurodonty, also present in *Parapedetes namaquensis*, but it cannot belong to this species on account of the much greater hypsodonty and curved columns of the latter species. In *Oldrichpedetes brigitteae*, the ratio H/L is 2.55.

Species *Oldrichpedetes praecursor* nov.

Holotype: KNM ME 10525, left M3/ from Meswa Bridge, Kenya. Type locality. Meswa Bridge, Kenya.

Age: Early Miocene age, ca 22.5 Ma (= MN 2).

Diagnosis: Extremely small pedetid, transverse lophs incomplete in unworn teeth, extremely brachyodont.

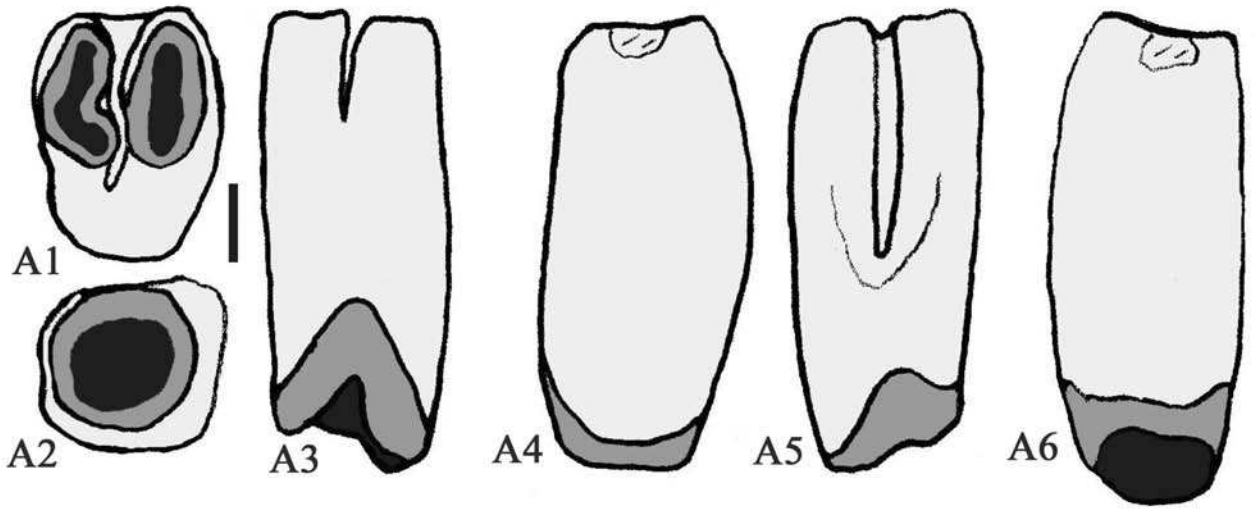

Fig. 12.—GSN ZH 1'95, left m/1 or m/2, holotype of *Oldrichpedetes brigitteae* from Zebra Hill, Namib-Naukluft Park, Namibia, A1) occlusal, A2) radicular, A3) buccal, A4) mesial, A5) lingual A6) distal views (scale - 1 mm).

Table 5.—**Measurements (in mm) of the teeth of *Oldrichpedetes brigitteae* nov. gen. nov. sp.**

Specimen	Tooth	MDL	blm	bld	H	S	s	H-s/L	H-S/L	S-s	H/L
GSN ZH 1'95	m/1 or m/2 left	2.23	2.14	2.17	5.77	3.55	1.28	0	0	2.27	2.55

Derivatio nominis: The species name refers to the primitive morphology of the type specimen and its possible role as an ancestor of later species in the genus.

Differential diagnosis: Differs from other species of *Oldrichpedetes* by its smaller dimensions, and its more brachyodont cheek teeth.

Description: The type specimen is a left M3/ comprising three cusps separated by narrow grooves, forming two lophs (Winkler, 1992) (Fig. 13, Table 6). The anterior loph is the widest part of the tooth. There is a narrowing between the loph and the protocone, marked on the mesial surface of the tooth as a narrow groove which would disappear with slight wear. There is also a narrowing on the posterior loph marked by a stronger posterior groove. The posterior loph is slightly oblique towards the rear and is shorter than the anterior loph. The enamel is relatively thick. There is an anterior contact facet towards the lingual side of the tooth. The roots are coalescent near the cervix, but are separated at their apices. The ratio H/L is 0.85.

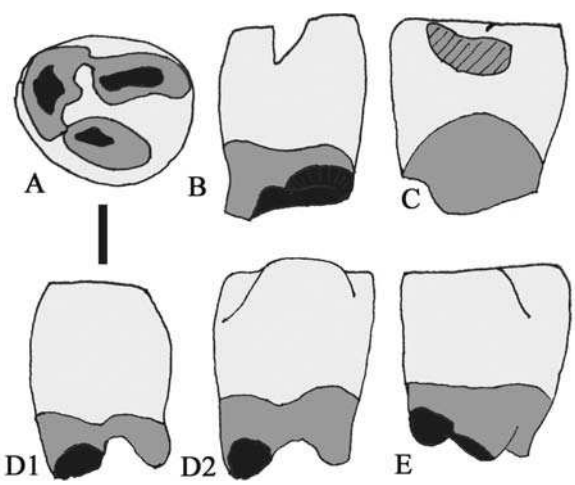

Fig. 13.—KNM ME 10525, holotype left M3/ of *Oldrichpedetes praecursor*, nov. gen. nov. sp. from Meswa Bridge, Kenya, A) occlusal, B) buccal, C) mesial, D1) distal, D2) distal oblique, and E) oblique lingual views (scale – 1 mm).

Discussion

The four species of *Oldrichpedetes* are distinguished from each other on the basis of dimensions of cheek teeth and their hypsodonty. The difference in height of the stria(id) does not change much through the geological record, unlike the genus *Pro-*

Table 6.—**Measurements (in mm) of the teeth of *Oldrichpedetes praecursor* nov. gen. nov. sp.**

Specimen	Tooth	MDL	blm	bld	H	H/L
KNM ME 10525	M3/ left	2.50	2.90	2.30	2.14	0.85

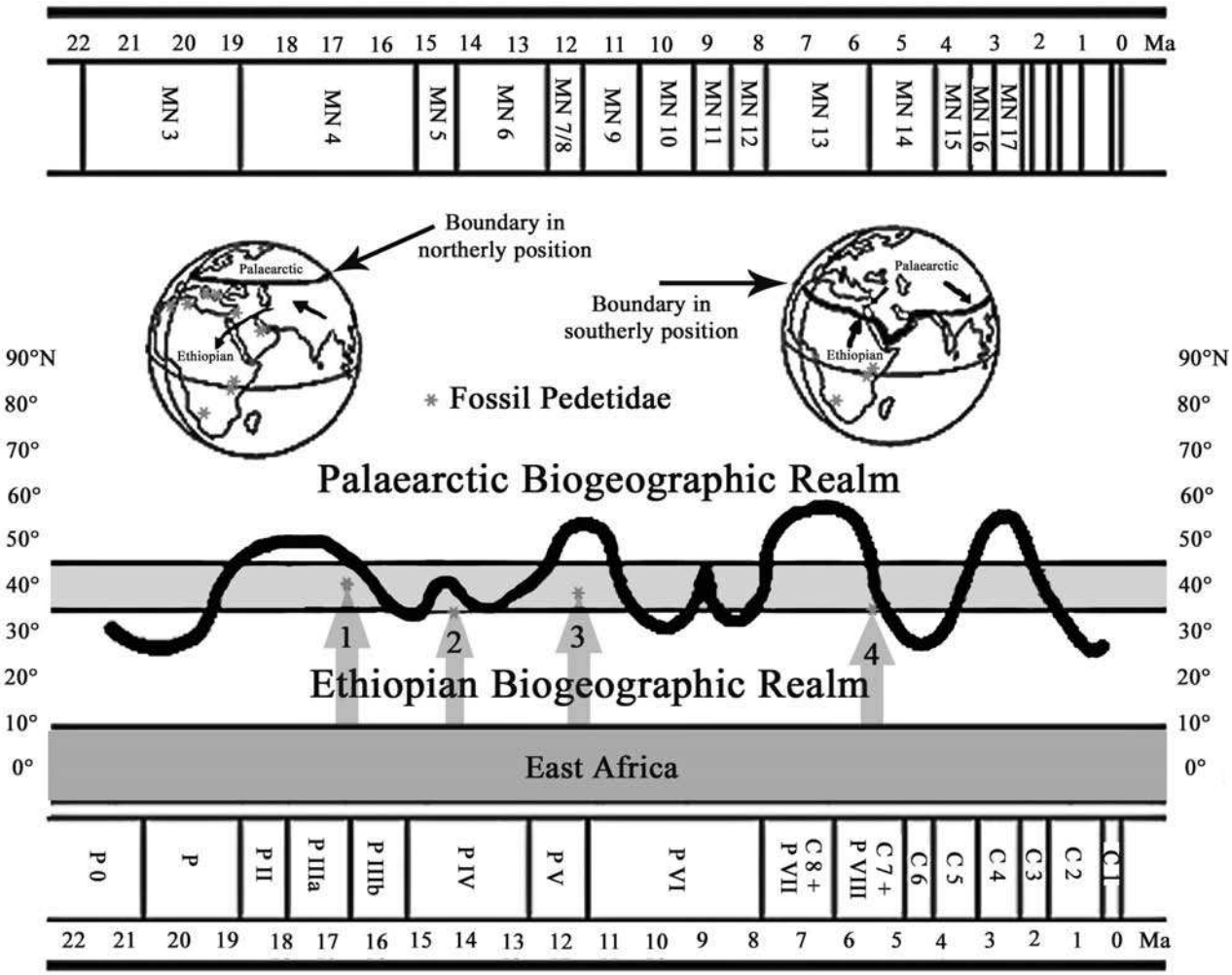

Fig. 14.—Northwards migration of Pedetidae during the Miocene (arrows marked 1 to 4) accords reasonably well with the movements of other mammals and plants during the period.

pedetes in which the dimension S-s increases steadily from ca 21 Ma to 3.5 Ma.

Biogeography

Pedetids are currently found only in the equatorial and austral zones of Africa (MacDonald, 2001) but it has been known for half a century that the family spread far northwards into the Arabian Peninsula, the Maghreb and even to southern Europe (Fig. 14) (Tobien, 1968).

An interesting point about the greater latitudinal range that the family had during the Miocene and Pliocene than it does today is that the septentrional records coincide with periods during which proto-Ethiopian faunas and floras spread northwards into mid-latitude Eurasia (MN 4, MN 5, MN 9 and MN 14). These were periods during which southern Europe was more tropical than it is today, with mammals such as tapirs appearing in the fossil record of Europe for example. During other periods, when mid-latitude Eurasia was under boreal palaeoclimatic conditions, plants and animals adapted to tropical environments disappeared from most of Europe as the boundary zone between the proto-Ethiopian and proto-Palaearctic Realms withdrew equator-wards (Fig. 14). As such the pedetids provide confirmation of the patterns of Mio-Pliocene faunal change summarised by Pickford & Morales (1994).

From time to time the faunal resemblance between East Africa and Spain was high, at other times low (diagram modified from Pickford &

Morales, 1994) reflecting latitudinal shifts in the position of the boundary between the proto-Ethiopian and proto-Palaearctic Zoogeographic Realms.

Conclusions

Fossils collected during the past two decades in Namibia and elsewhere in Africa have revealed that the rodent family Pedetidae is more diverse than previously thought. Until 2008, only three genera had been reported in the literature, *Pedetes* (the extant genus), *Parapedetes* (known from a single site in Namibia) and *Megapedetes* (widespread in equatorial East African Early and Middle Miocene sites, and reported from North Africa, the Arabian Peninsula and southern Europe. Recently the genus *Propedetes* was described, and this paper erects two new genera, *Rusingapedetes* and *Oldrichpedetes*, bringing to five the diversity of the family at the generic level. Both *Propedetes* and *Oldrichpedetes* comprise several species which evolved rapidly in terms of hypsodonty, such that they are of potential use for biochronology. *Propedetes* in particular is likely the ancestral lineage from which the extant genus *Pedetes* emerged during the Pliocene, the transition from the former to the latter being defined in the main by the non-development of roots in the cheek teeth in the latter.

Pedetids throw light on the biogeographic and palaeoclimatic relations of North Africa, the Arabian Peninsula and parts of Southern Europe during certain periods of the Miocene and Pliocene, revealing the establishment of tropical to subtropical regimes in mid-latitude Eurasia from time to time.

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